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RESEARCH ARTICLE

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# Predictive modelling of mesophotic habitats in the north-western Gulf of Mexico

Travis Keenan Sterne[1] | David Retchless[1] | Rebecca Allee[2] | Wesley Highfield[1]

[1]Department of Marine Sciences, Texas A&M University Galveston, Galveston, TX

[2]NOAA Office for Coastal Management - Gulf Region, Stennis Space Center, MS

**Correspondence**
Travis Sterne, 3837 FM 1685, Victoria, TX 77905, USA.
Email: travis.sterne17@gmail.com

## Abstract

1. Effective management of marine resources requires an understanding of the spatial distribution of biologically important communities.
2. The north-western Gulf of Mexico contains diverse marine ecosystems at a large range of depths and geographic settings. To better understand the distribution of these marine habitats across large geographic areas under consideration for marine sanctuary status, presence-only predictive modelling was used.
3. Results confirmed that local geographic characteristics can accurately predict the probability of occurrence for marine habitat types, and include a novel technique for assigning a single, most likely habitat in areas where multiple habitats are predicted.
4. The highest resolution bathymetric data (10 m) available for the region was used to develop raster layers that represent characteristics that have been shown to influence species occurrence in other settings.
5. A georeferenced historical photo record collected via remotely operated vehicle was classified according to six commonly found mesophotic habitats across the 18 reefs and banks under consideration for Flower Garden Banks National Marine Sanctuary boundary expansion.
6. Using maximum entropy modelling, the influence of local geographic characteristics on the presence of these habitats was measured and a spatial probability distribution was developed for each habitat type across the study area.

KEYWORDS
benthos, coral, fishing, habitat mapping, modelling, ocean, trawling

## 1 | INTRODUCTION

Resource management is becoming increasingly urgent as humans continue to place heavier pressure on the finite stocks of living and non-living resources. Mostly due to the limitations of common research methods, coral reef distribution known to the scientific community is primarily limited to the dense assemblages of shallow reef-building corals. However, diverse coral ecosystems exist in deep waters of continental shelves, slopes, seamounts, and ridges. These habitats contain fragile and slow-growing species of lesser-known invertebrates, some of which serve as proxies for environmental conditions over millennia (Etnoyer et al., 2018; Roberts, Wheeler, & Freiwald, 2006).

Marine Protected Areas (MPAs) are established to allow marine species and their habitats to exist and reproduce without human interaction, reducing their vulnerability to exploitation and climate change (Office of National Marine Sanctuaries [ONMS, 2016). To aid in the identification of potentially sensitive biological communities or expansion of MPAs, resource managers need to know the spatial distribution of conservation priorities. It is not economically efficient to survey every environment with great detail, particularly those that exist in the deepest waters of the ocean.

  

By combining information on the observed habitat locations with spatial predictors, the spatial association between the presence of biota and local geographic characteristics can be modelled across space (Baker & Weber, 1975; Guisan & Zimmermann, 2000; Pittman, Costa, & Battista, 2009; Stolt et al., 2011). Founded on ecological niche theory, predictive habitat and species distribution modelling of mesophotic communities provides a rapid and cost effective tool for predicting large-scale distribution, the effects of human use, and environmental change (Guisan & Zimmermann, 2000; Hirzel, Helfer, & Metral, 2001; Phillips, Anderson, & Schapire, 2006; Pittman & Brown, 2011). Data for predictive modelling of biological communities may come from several sources, including imagery from exploratory remotely operated vehicle (ROV) operations conducted in marine environments by various governments, private companies, and academic institutions.

This project developed an ROV-based approach to predictive habitat modelling in ocean-floor environments and evaluated its suitability and effectiveness for mesophotic environments in the north-western Gulf of Mexico. Specifically, the project addressed: (1) how well local geographic characteristics predict the presence of marine habitats in the north-western Gulf of Mexico; (2) given this, where are habitats predicted to occur in the region; and (3) important policy and planning implications of the results.

### 1.1 | Hypothesized relationships between geographic characteristics and habitat types

With the exception of soft bottom environments, the habitats in this study are largely characterized by the benthic taxa they contain. Recent studies have shown geographic characteristics to be statistically significant predictors of coral and algae species; it is therefore inferred that they can be used to predict occurrence of the habitats in which they thrive. For example, in applying this surrogate approach to coral habitats, scleractinian coral presence indicates Coral Reef or Coral Community habitat (depending on density), dense crustose coralline algae (CCA) cover indicates Algal Nodule or CCA Reef (depending on morphology), and substrate inhabited by antipatharian and octocoral species indicates Deep Coral habitat (Schmahl, Hickerson, & Precht, 2008). It is also inferred that local geographic characteristics capable of influencing probability of occurrence for species (scleractinians, crustose coralline algae, antipatharians, octocorals) within one habitat (Coral Reef, Algal Nodule, Algal Reef, or Deep Coral) have a high potential to affect the probability in others.

Prior research suggests likely relationships between geographic characteristics and benthic ecology in environments characterized by coral and algae species. Depth is well known to influence the growth rate of coral and algae species (Adey, 1966, 1970; Adey & Macintyre, 1973; Baker & Weber, 1975; Bosellini & Ginsburg, 1971; Minnery, 1990; Minnery, Rezak, & Bright, 1985; Rezak, Bright, & McGrail, 1985). In general, habitats that are characterized by photosynthesizing organisms such as hermatypic corals and CCA are expected to share an inverse relationship with depth, given that it limits the amount of available light needed for their progression due to refraction and turbidity caused by suspended sediments (Adey, 1966, 1970; Adey & Macintyre, 1973; Baker & Weber, 1975; Bosellini & Ginsburg, 1971; Minnery, 1990; Minnery et al., 1985; Rezak et al., 1985). Antipatharians and octocorals that characterize deep coral habitats benefit from the lack of competing, faster-growing benthic species such as CCA and need much lesser amounts of light to grow. Thus, these habitats would be likely to share a positive correlation with depth.

Bottom slope, rugosity, and plan curvature capture the geographic complexity of a specific area. Prior research has shown a strong correlation between these three metrics and the occurrence of hard coral species and associated fish communities (Pittman et al., 2009; Wedding & Friedlander, 2008); these metrics have also been examined as predictors of species richness and abundance (Anderson et al., 2016; Lecours, Lucieer, Dolan, & Micallef, 2018; Pittman & Brown, 2011; Pittman et al., 2009; Wedding & Friedlander, 2008; Young & Carr, 2015). Thus, it was expected that all habitats characterized by high morphometric complexity would share a positive correlation with the presence of coral habitats.

Aspect represents the compass direction in which a given sloping area faces. This parameter has not been well-documented to have substantial influence on the occurrence of species found within these habitats, and the results of this model were not expected to be greatly influenced by it. However, past research has shown that current velocity, a parameter that is often determined by aspect, has a direct influence on some species included in the modelled habitats (Adey, 1966, 1970; Adey & Macintyre, 1973; Minnery, 1990).

Soft Bottom habitats are known to occur primarily on low-lying, level geographic features in the north-western Gulf of Mexico. The sediments that make up the sea floor in these habitats are primarily terrigenous and calcareous in nature, resulting from coastal river outflows and skeletal remains of planktonic organisms (Schmahl et al., 2008). Given the relatively featureless characteristics of these habitats, they were expected to be found in areas with minimal local relief (rugosity), slope of slope, slope, and plan curvature. Areas with high values for these co-variables were expected to decrease the probability of Soft Bottom habitat occurrence.

In line with this literature, hypotheses were made about each geographic characteristic-habitat type relationship. Table 1 defines the relationships expected to be found between each habitat and associated geographic characteristics. The relationships between these geographic characteristics and the presence of specific Flower Garden Banks National Marine Sanctuary (FGBNMS) habitat types are discussed in Appendix 1.1 in more detail.

## 2 | MATERIALS AND METHODS

### 2.1 | Background: Study site and associated habitat types

At present, FGBNMS protects only three of the many reefs and banks located on the edge of the continental shelf in the Gulf of

**TABLE 1** Predicted and observed influence of covariates on probability. This table represents the predicted relationship (+/–) and expected strength of co-variate influence (•) for each habitat within the model. This does not represent specific quantitative significance levels; '•' to '•••' represents the strength of the expected relationship. Predicted levels of influence for each covariate represent qualitative assessments of likely relationships based on cited literature results and the researchers' *in situ* observations, and should not be confused with statistical significance levels

| | Predicted/Observed | Depth | Slope | Slope of Slope | Rugosity | Plan Curvature | Aspect (S → N) † | Aspect (W → E) † |
|---|---|---|---|---|---|---|---|---|
| **Coral Reef** | Predicted | - (•••) | + (••) | + (•••) | + (•••) | + (•••) | • | • |
| | Observed | - (•••) | + (••) | + (••) | + (••) | + (•) | • | • |
| **Coral Community** | Predicted | - (•••) | + (••) | + (•••) | + (•••) | + (•••) | • | • |
| | Observed | - (•••) | + (•••) | + (•••) | + (•••) | + (•••) | • | • |
| **Algal Nodule** | Predicted | + (•••) | - (••) | - (••) | - (••) | - (••) | •• | •• |
| | Observed | - (•••) | + (•••) | + (•••) | + (•••) | + (••) | • | • |
| **Algal Reef** | Predicted | + (•••) | + (••) | + (•••) | + (•••) | + (•••) | •• | •• |
| | Observed | - (•••) | + (•••) | + (•••) | + (•••) | + (••) | • | • |
| **Deep Coral** | Predicted | + (•••) | + (••) | + (•••) | + (•••) | + (•••) | • | • |
| | Observed | + (••) | + (•••) | + (•••) | + (•••) | + (•••) | • | • |
| **Soft Bottom** | Predicted | + (•••) | - (••) | - (••) | - (••) | - (••) | • | • |
| | Observed | + (••) | N/A (•••) | + (•••) | N/A (•••) | N/A (••) | • | • |

†Specific relationships (+/–) for this variable are not included in this study.

Mexico: East and West Flower Garden Bank, and Stetson Bank. NOAA has proposed adding 15 underwater areas located 113–161 km from the coastlines of Texas and Louisiana to the existing sanctuary. Should the proposed expansion into these areas be adopted, the total area would increase from 145 to 992 km$^2$ (Figure 1). These underwater features include: Horseshoe, 28 Fathom, MacNeil, Rankin, Bright, Geyer, Elvers McGrail, Bouma, Bryant Rezak, Sidner, Sonnier, Alderdice, and Parker Bank. According to the Gulf of Mexico Ecosystem Restoration Task Force, these areas are listed as ecologically significant sites that should be protected and managed to maintain overall biological productivity and resilience (Office of National Marine Sanctuaries [ONMS], 2016). All of these areas have been the focus of exploratory ROV expeditions, which have recorded data used not only to measure species richness and abundance but also to describe bottom types via in-situ annotations.

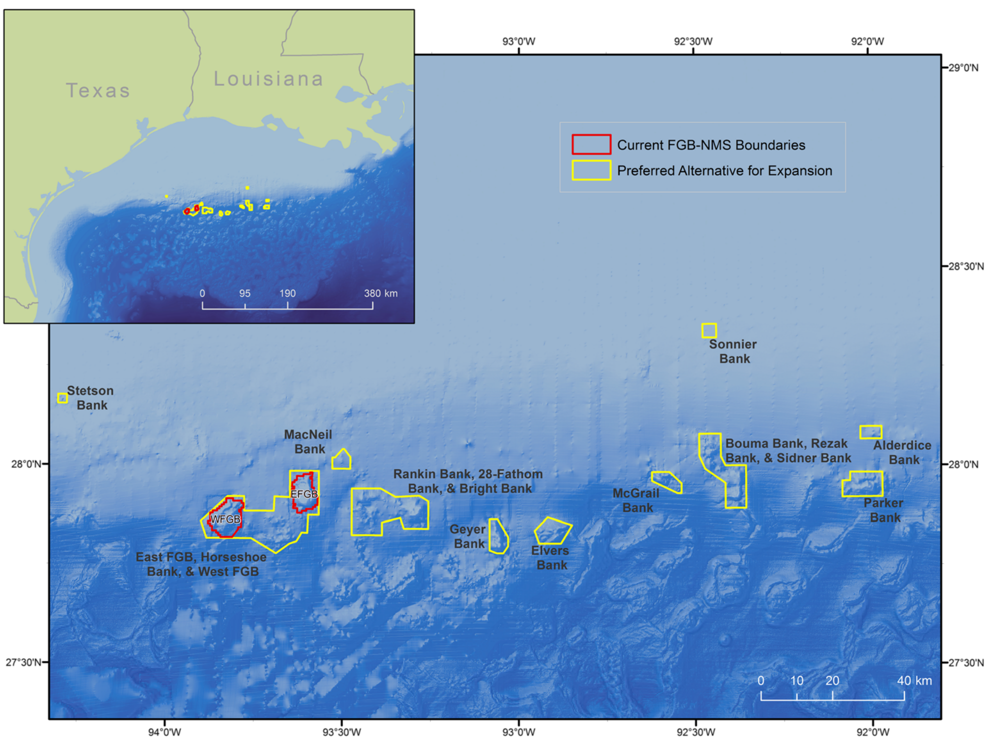


**FIGURE 1** Flower Garden Banks National Marine Sanctuary (FGB-NMS) and the preferred alternative boundary expansion alternative as per the Draft of the Environmental Impact Statement (DEIS) prepared by Office of National Marine Sanctuaries [ONMS] 2016

Over the course of this research, ROV-based habitat observations have been recorded under a localized FGBNMS classification scheme. The habitat categories under this scheme include: Coral Reef, Coral Community, Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom habitat – all of which refer to commonly-found ecosystems in the north-western Gulf of Mexico. These habitat descriptions are useful in communicating observations internally as well as to the general public and affiliated stakeholders in the region. Accordingly, this research primarily used this localized FGBNMS classification scheme. National-level classification schemes such as the Coastal and Marine Ecological Classification Standard (CMECS) may also be applied to FGBNMS habitats (Carollo, Allee, & Yoskowitz, 2013; Federal Geographic Data Committee, 2012; Ruby, 2017); an explanation of how the FGBNMS and CMECS scheme are inter-related can be found in the Appendix (Table A1).

## 2.2 | Data collection and photo analysis

A probability distribution predicting the likelihood of occurrence for six commonly observed habitat types in the north-western Gulf of Mexico was generated using: (1) photographic ROV data collected by NOAA FGBNMS; and (2) local geographic characteristics extracted from high-definition bathymetry data using Environmental Systems Research Institute (ESRI) ArcMap mapping software. Field data collection for this project included 16 years (2001–2016) of collaboration between FGBNMS and the University of North Carolina Wilmington's Undersea Vehicles Program. Two different models of ROV were used to collect data utilized for this model. A description of each model can be found in the Appendix (Table A2). Approximately 7,150 geo-referenced photographs analysed by FGBNMS scientists during previous habitat classification research (Sammarco et al., 2016) were combined with the entire mesophotic photo record from FGBNMS expeditions in the north-western Gulf, totalling 19,514 photos. These photos were geo-referenced using post-processing procedures that use the photos' timestamps and information about the ROV's speed to correct for gaps in location data from the ROV Hypack GPS (approximately 10% of photos were so corrected, introducing an additional horizontal error of up to 1.03 m; Appendix 2.2.1).

Still images from each dive were reviewed to determine their usability for qualitative analysis. If at least 50% (approximate) of the photo could be analysed for benthos, it was used in the primary data analysis for the project. Usable photos were classified according to the regional FGBNMS habitat scheme based on the qualitative analysis to detect the presence of any definitive species, as well as substrate type that characterize the habitats of interest, using Windows Photo Viewer. The defining characteristics of each habitat type were found in the guidance documents for each respective classification category (Federal Geographic Data Committee, 2012; Schmahl et al., 2008). Under the FGBNMS scheme, a photo has a classification for Biological Zone and Major Habitat (Table A1). Each usable photo was assigned to one of the six FGBNMS habitats considered in this study; this habitat code was stored along with its latitude and longitude in a comma separated value (.csv) file. These data points served as the occurrence records that maximum entropy (MaxEnt) used to construct the spatial probability distribution across the study area. Data points used to develop the probability distribution include 238 Coral Reef, 203 Coral Community, 1,431 Algal Nodule, 4,178 Algal Reef, 4,746 Deep Coral, and 8,718 Soft Bottom classifications.

## 2.3 | Bathymetric data

Digital terrain models derived from high-definition multibeam acoustic sensor data were used to quantify spatial predictors representing a range of variables of seafloor morphology. Since 2002, these bathymetric data have been collected by a coalition of FGBNMS, Bureau of Ocean Energy Management (formerly known as Minerals Management Service), and US Geological Survey.

Raster surfaces derived from the bathymetric data obtained for this project were projected in WGS 1984 UTM Zone 15 N coordinate system. The original resolution of the bathymetry data being used for this research ranges from approximately 1–8 m. To account for the coarsest resolution of the original data (8 m) and the error in the ROVs' horizontal position during data collection, ESRI's Resampling tool for ArcMap was used with a bilinear resampling technique (ESRI, 2017) to standardize the resolution of each raster dataset to a 10 m × 10 m cell size. The 18 multibeam datasets were compiled into one single-band raster layer with 32-bit floating point pixel type using ArcMap's Mosaic to New Raster Tool.

Based on a review of the literature, depth, bottom slope, slope of slope, rugosity, plan curvature, and aspect are the characteristics most likely to predict presence of FGBNMS habitat types. These were therefore the characteristics that were used as environmental covariates to estimate habitat distribution in this study. The raster mosaic served as both the depth raster and the base raster surface from which all remaining environmental parameters for this project were calculated. Five morphometric transformations of the depth surface layer were generated in ArcMap software:

- Slope (maximum rate of change in the three-by-three cell neighbourhood; Slope tool with depth as input);
- Slope of slope (maximum rate of slope change in the three-by-three cell neighbourhood; Slope tool with slope as input);
- Rugosity (the secant of slope in radians, equivalent to 3D to 2D area ratio, for each grid cell; Raster Calculator tool, as described in Rinehart et al., 2013);
- Plan curvature (the horizontal convexity or concavity of a sloping pixel; Curvature tool);
- Aspect variation (direction each grid cell faces; Aspect tool output vectorized on 0–1 scales to westerly and southerly components, each evaluated independently).

Following their creation, each file was converted into an ASCII grid layer, as is required by MaxEnt.

### 2.4 | MaxEnt modelling

Habitat suitability modelling has been widely used to predict the distribution of number of deep-sea and cold-water scleratinians, octocorals, and antipatharians in order to more comprehensively understand shelf habitats and aid resource management decisions regarding their protection (Krigsman, Yoklavich, Dick, & Cochrane, 2012; Rengstorf, Yesson, Brown, Grehan, & Crame, 2013; Tazioli, Bo, Boyer, Rotinsulu, & Bavestrello, 2007; Woodby, Carlile, & Hulbert, 2009). For this project, habitat suitability was predicted using the MaxEnt estimation method, which was developed for modelling species' geographic distributions (Elith et al., 2010; Phillips et al., 2006; Phillips & Dudík, 2008). Specifically, this modelling approach offers the most random distribution of each habitat type across the full extent of the study area consistent with the covariate values (depth, slope, slope of slope, plan curvature, rugosity, and aspect) observed at each ROV-observed sample point. This results in the least-biased estimate given the region(s) of phase space included in the available information (Jaynes, 1957). MaxEnt uses independent variables, or covariates, from a sample record for each habitat, along with a sample of background points from an ASCII raster grid that represents a geographic region, to independently estimate a spatial probability distribution for each habitat occurrence (Elith et al., 2010; Phillips et al., 2006).

### 2.5 | MaxEnt outputs

#### 2.5.1 | Receiver operating characteristic

A major concern of ecological modelling is the accuracy of a model in predicting the presence and/or absence of some organism or habitat. MaxEnt allows a subset of data to be set aside for an independent accuracy assessment called the receiver operating characteristic. This test refers to a measure of model accuracy in terms of its ability to correctly predict the occurrence of a given habitat type; it is a function of the proportion of error in testing the model with a random subset of data (Deleo, 1993; Fielding & Bell, 1997). In the case of MaxEnt modelling, the ratio represents the ability of the model to identify presence relative to a completely random distribution (Phillips et al., 2006). This ratio is also known as *sensitivity*. The area underneath this receiver operating characteristic curve (AUC score) is equal to the probability that a randomly chosen positive instance and a randomly chosen locality with probability equal to zero are correctly predicted by the model.

### 2.6 | Response curves

MaxEnt response curves illustrate the probability response for each habitat type as predictor values vary. Each plot is developed by creating a model using only the corresponding environmental predictor (Phillips, 2017). The patterns represented by the curves are useful for comparative analysis between habitat types and their relative response to increasing/decreasing values of each predictor.

#### 2.6.1 | Percentage contribution and permutation importance

These metrics present the relative estimates of model contribution by each environmental predictor. The second estimate (permutation importance) is calculated by taking the presence data used for training and background samples and running a random permutation using each variable in turn. The software then records the successive drop in AUC during each permutation to determine importance as a percentage. The jackknife test of variable importance gives further insight by evaluating the relative influence of each environmental predictor independently.

The value of variable contribution or permutation importance is indicative of the degree to which the presence of each respective habitat is dependent upon each variable; a high value indicates high dependability, and vice-versa. In some cases, the relative contribution to model performance is increased or decreased substantially between variable contribution and permutation importance. A shift from a high contribution score to a substantially lower permutation score may be the result of multi-collinearity among covariates (Baldwin, 2009). The permutation process of MaxEnt highlights these relationships and the regularization of the model algorithm protects overall model performance from this effect (Bradie & Leung, 2016; Cruz-Cárdenas, López-Mata, Villaseñor, & Ortiz, 2014).

#### 2.6.2 | Spatial probability distributions

In the final step of the modelling process, MaxEnt produces a spatial probability distribution for each habitat type across the study area. It builds a raster grid (.ASC) for each habitat in which each pixel represents the probability (0–1.0) for it to occur.

#### 2.6.3 | Mapping MaxEnt probabilities using multinomial logistic regression

For habitat prediction and management applications of the MaxEnt model output, it is important to illustrate the spatial distribution of each habitat type in relation to others. To do this, the probability distributions for all habitat types were combined using ArcMap raster calculator. A major challenge in combining habitat types was presented by areas where MaxEnt predicts more than one type of habitat to occur with probability >50%; in this project, these areas were termed 'transitional zones.' To maximize the statistical accuracy of the model, a multinomial logistic regression (MLR) analysis using both the MaxEnt probability distributions for each habitat (independent variables) and sample observation point data (dependent variable) was used to find which MaxEnt habitat type probabilities were more

**TABLE 2** Scenario description for outcome decisions

| Scenario | Coefficient of var *a* (log of the odds of observing *a* relative to the odds of observing *b*) | Coefficient of var *b* (log of the odds of observing *b* relative to the odds of observing *a*) | Result |
|---|---|---|---|
| 1 | Positive; $p \leq 0.05$ | Positive; $p \leq 0.05$ | Location assigned to habitat with highest maximum entropy probability. |
| 2 | $p \leq 0.05$; positive | $p \geq 0.05$ and/or negative | Location assigned to var *a*. (Inverse situation = *b*) |
| 3 | $p \geq 0.05$ and/or negative | $p \geq 0.05$ and/or negative | Habitat type considered transitional. |

predictive of the habitats actually observed at the sample points (classified ROV imagery) within each transitional zone.

This allowed the development of a rule set for breaking ties in transitional zones, with the goal of assigning grid cells in these areas to a single habitat type from among the two or more habitat types predicted with high probability at that location. Table 2 contains the MLR-based guidelines on which decisions were made to assign categorical values to pixels of overlapping habitats with high probability. These distributions were combined so as to qualitatively and quantitatively realize the relative spatial relationships between the mesophotic habitats across the study area. A more comprehensive description of the methods used to process transitional areas can be found in the Appendix 3.1.2.

## 3 | RESULTS

### 3.1 | AUC and overall model performance

The AUC scores for Coral Reef Coral Community, Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom habitat were 0.988, 0.995, 0.944, 0.901, 0.876, and 0.798, respectively. These results showed that, relative to the other models, the Coral Community model performed best according to the random test sample (25%) set aside from the observation data. That is, this model correctly identified Coral Community presence 99.5% of the time.

#### 3.1.1 | Percentage contribution and permutation importance

Depth showed the strongest contribution to model gain, especially for Coral Reef habitats (Table 3). It also showed the highest permutation importance across all habitats. It is important to note that its permutation importance increased relative to variable contribution across all habitats, indicating that depth was minimally or unaffected by multicollinearity between variables in this model (Baldwin, 2009). Slope of slope substantially contributed to the model, primarily for Algal Reef and Deep Coral habitats, although its importance decreased when used as the only predictor. Slope was also a relatively important contributor to overall model performance, especially for deeper habitats; however, model gain decreased substantially in

**TABLE 3** Variable contribution and permutation importance

| Habitat | Depth | Slope | Slope of slope | Rugosity | Plan curvature | Aspect (S-N) | Aspect (W-E) |
|---|---|---|---|---|---|---|---|
| Variable contribution (%) | | | | | | | |
| Coral Reef | 96.4 | 2.3 | 0.3 | 0.4 | 0.0 | 0.5 | 0.0 |
| Coral Community | 76.0 | 2.3 | 3.6 | 16.9 | 0.1 | 0.2 | 0.3 |
| Algal Nodule | 49.4 | 33.6 | 6.6 | 10.1 | 0.0 | 0.3 | 0.1 |
| Algal Reef | 33.6 | 26.9 | 38.1 | 0.6 | 0.6 | 0.1 | 0.0 |
| Deep Coral | 11.8 | 17.0 | 67.0 | 0.2 | 4.0 | 0.0 | 0.0 |
| Soft Bottom | 28.5 | 30.0 | 38.4 | 0.9 | 0.7 | 0.0 | 0.1 |
| ***Average Contribution*** | 49.3 | 18.7 | 25.7 | 4.9 | 0.9 | 0.2 | 0.1 |
| ***Permutation Importance*** | | | | | | | |
| Coral Reef | 98.5 | 0.0 | 0.0 | 0.8 | 0.0 | 0.6 | 0.0 |
| Coral Community | 99.0 | 0.0 | 0.1 | 0.8 | 0.0 | 0.0 | 0.0 |
| Algal Nodule | 76.1 | 14.8 | 1.5 | 7.3 | 0.0 | 0.1 | 0.1 |
| Algal Reef | 73.8 | 0.5 | 12.6 | 12.5 | 0.5 | 0.1 | 0.0 |
| Deep Coral | 32.2 | 1.8 | 52.2 | 9.5 | 3.2 | 0.1 | 0.1 |
| Soft Bottom | 54.5 | 3.2 | 20.9 | 15.5 | 0.9 | 0.0 | 0.1 |
| ***Average importance*** | 72.4 | 3.4 | 14.5 | 7.7 | 0.8 | 0.2 | 0.1 |

permutations using this variable alone. While rugosity appears to have had little relative influence on overall model performance, AUC scores recorded during permutations indicated an interesting shift from very low to moderate importance in model gain for Algal Reef, Deep Coral, and Soft Bottom habitats. Using this metric for variable contribution to the model, all other variables showed minimal influence.

## 3.2 | Response curves

For depth, response curves showed that probabilities for habitats characterized by dense assemblages of light-dependent species (such as hermatypic corals and photosynthesizing algae) were higher in shallower areas, while Algal Nodule, Algal Reef, and particularly Deep Coral habitats showed peaks in probability in deeper water (Figure 2). Slope appeared to have high initial influence as it increased from zero at the low end, though its effect gradually decreased for high slope values, having either a slight negative (Coral Reef, Coral Community, and Algal Nodule) or slightly positive (Algal Reef, Deep Coral, Soft Bottom) effect on occurrence probability in this range. The curves for slope of slope and rugosity showed similar response patterns. For planform curvature, Coral Community showed lower probabilities for convex features (negative values) and higher probabilities for concave features (positive values). The probability response for planform curvature for the remaining habitats in the model all presented a relatively constant probability >0.70 for convex features, with a slightly higher probability prediction for concave features, and a dip in probability to 0.40 or lower for flat features. For aspect, probabilities appeared to be slightly higher for northerly and easterly facing areas.

## 3.3 | Maps of likely habitat locations

As one would expect to find, Coral Reef and Coral Community habitats were estimated to occur primarily around the shallowest features

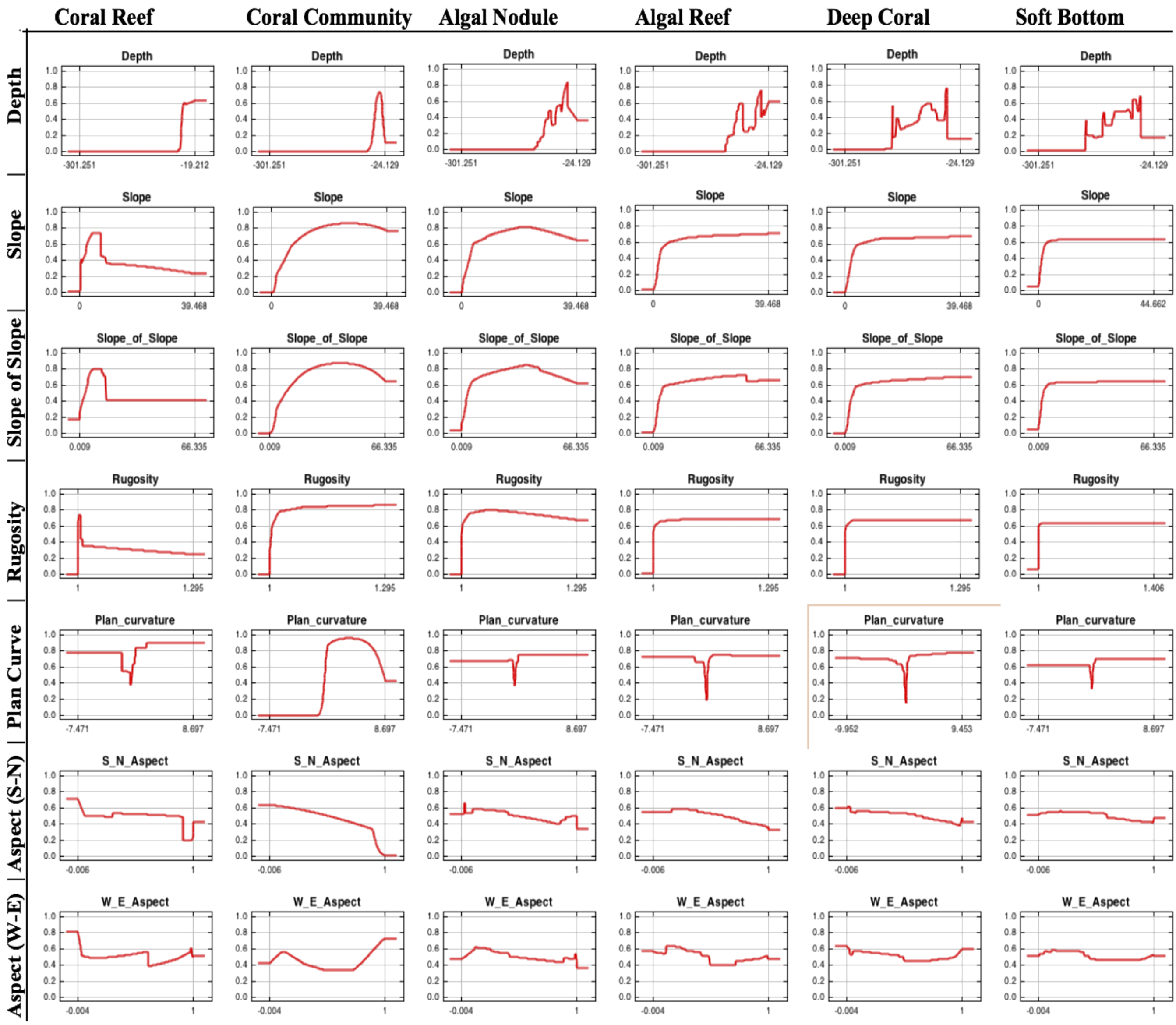


**FIGURE 2** Response curves. The curve represents a model using only the corresponding variable

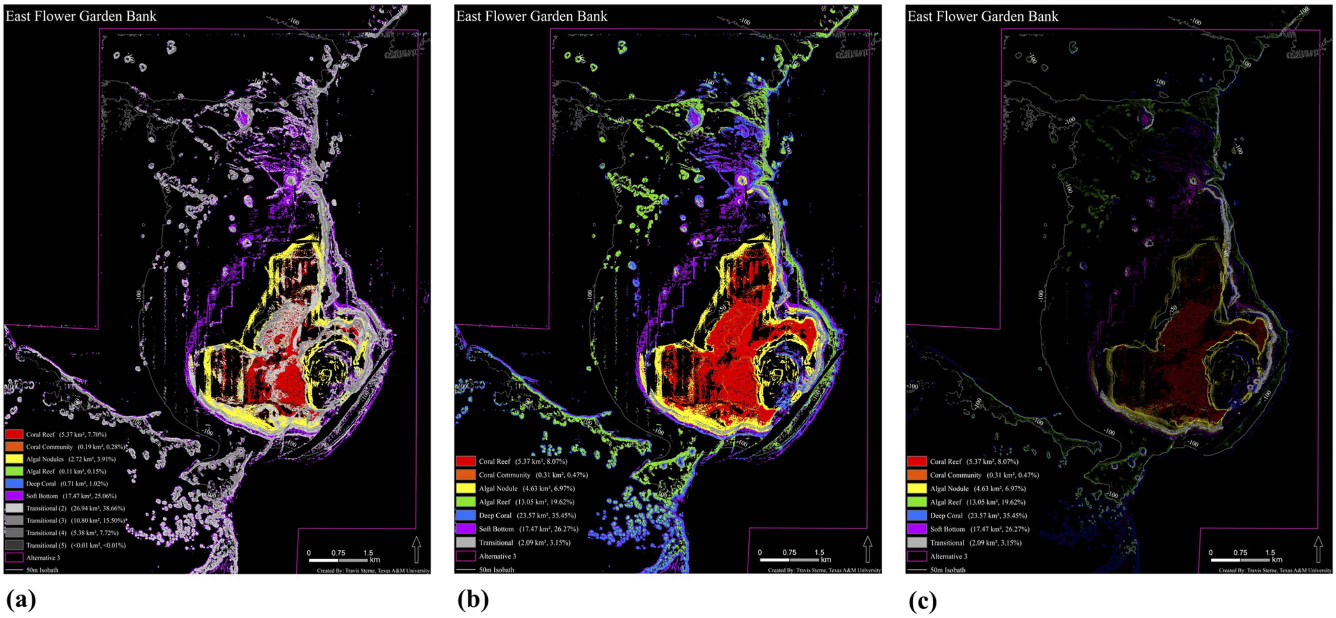


**FIGURE 3** Sequence of probability distributions: (a) represents the distribution of habitats across East Flower Garden Bank including four degrees of overlapping area predicted with high probability; (b) represents the resulting distribution of habitats following selection of primary habitat type via multinomial logistic regression, as outlined in Section 2.6.3; and (c) represents the final distribution of habitats with the highest probability of occurrence, mapped with opacity indicating the degree of confidence that the model has in predicting occurrence

of the study area; the general patterns of Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom distributions appear less definitive (Figure 3). In an initial assessment of these raster surfaces, substantial overlap in the spatial distribution of high-probability (>0.50) for occurrence of each habitat type were observed, with many instances in which MaxEnt assigned a high probability for two, three, four, and occasionally five types of habitats to occur in the same location. Table A4 identifies all combinations of overlapping habitat types, the total area they cover, and the outcome of applying MLR-based guidelines (Table 2) for each case. Figure 3 illustrates the distribution of these overlapping areas, as well as areas in which only one habitat was predicted to occur with high confidence, throughout East Flower Garden Bank. The final map, (Figure 3c), was rendered by combining the categorical raster grid of habitat types with their respective probabilities as assigned by MaxEnt; the opacity of each grid cell represents the probability that said habitat occurs. Table 4 quantifies total area covered by each habitat in the study area after addressing high probability discrepancies using MLR.

## 4 | DISCUSSION

In general, the results showed that local geographic characteristics provided accurate metrics for predicting the occurrence of the habitats of interest; the 18 reefs and banks included in the FGBNMS Expansion Proposal were predicted to contain networks of biologically important habitats (ONMS, 2016), and the results support this prediction. For each habitat, environmental predictors' influence in the MaxEnt model (as measured by variable contribution, permutation importance, and jackknife tests of variable importance) was compared to that set forth in the hypotheses and the findings of existing empirical studies. The implications of the results for the hypothesized influence of each environmental variable on FGBNMS habitat classifications are summarized in Table 1. Consistent with the hypotheses, the majority of predictive environmental variables included in the model were shown to have influence on the presence of Coral Reef, Coral Community, Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom habitats in the study area (Table 1; Figure 2).

### 4.1 | Effects of environmental predictors on habitat probability

#### 4.1.1 | Coral Reef and Coral Community

For Coral Reef and Coral Community habitats, the results supported the hypothesized decrease in probability with increasing depth. This was supported by the jackknife plots, which showed a large decline in model performance when depth was removed as an environmental predictor for these habitats. This observation is consistent with the relationship predicted to occur (Table 1) and conclusions of Baker and Weber (1975). Coral Reef and Coral Community are both characterized by the presence of photosynthesizing hard corals and other benthos and thus one would logically expect to find this relationship to hold true. According to the jackknife test data, the second most influential parameter for Coral Reef was slope of slope. For Coral Community, rugosity appeared to have high relative influence on habitat occurrence; however, when the permutations were performed, its relative influence decreased (Table 1). This indicated that, in the absence of other variables (primarily depth), rugosity did not have much

**TABLE 4** Total area of habitat coverage. Prior Area refers to total area prior to statistical transformation via multinomial logistic regression analysis (Prior Area) and Final Area represents high confidence habitat coverage by type following this transformation

| Habitat type | Prior area (km$^2$) | Final area (km$^2$) |
|---|---|---|
| Coral Reef | 5.53 | 5.93 |
| Coral Community | 0.24 | 0.48 |
| Algal Nodule | 3.93 | 9.31 |
| Algal Reef | 0.26 | 32.76 |
| Deep Coral | 3.36 | 59.12 |
| Soft Bottom | 53.93 | 53.93 |
| Transitional | 102.81 | 6.71 |

predictive power for this habitat. The results for planform curvature also indicated that Coral Community habitat was more likely to occur on laterally convex bottom features.

#### 4.1.2 | Algal Nodule and Algal Reef (CCA)

In the case of running the model without depth as a predictor, a substantial decrease in model performance was observed for both these habitats. This observation is consistent with the hypothesis and findings of Adey (1966, 1970) and Minnery (1990). These studies indicate that the presence of CCA is largely controlled by available light, temperature, and grazing herbivores (parrot fish) whose distribution is limited by depth and competing organisms such as hermatypic corals. Algal Nodule habitat was also shown be significantly influenced by degree of Slope. This is speculated to be a result of the general distribution of this habitat around prominent features where sunlight still penetrates the entire water column and waves and currents still influence the sea floor to a degree that allows the formation of nodules (Bosellini & Ginsburg, 1971; McMaster & Conover, 1966; Minnery, 1990; Rezak et al., 1985; Scoffin, Stoddart, Tudhope, & Woodroffe, 1985). For Algal Reef, slope of slope performed as the strongest environmental predictor when including all covariates in the model, while the omission of depth caused the largest decline in model performance; slope also showed substantial relative importance in predicting presence of this habitat (Table 1).

#### 4.1.3 | Deep Coral

Performance of the predictive model for Deep Coral declined when depth was excluded, indicating that it is a strong predictor of Deep Coral habitat. In line with this result, past research has indicated that the density of scleractinian and algal species decrease with depth, reducing competition and enabling gorgonian and antipatharian species characteristic of Deep Coral habitats to proliferate (Tazioli et al., 2007; Wagner, Luck, & Toonen, 2012). Comparatively, however, slope of slope provided the best predictive performance for this habitat in the overall model. This may be a result of reaching a minimum threshold of available light required by photosynthesizing benthos, at which point those species can no longer compete with deep coral species. Upon reaching this depth, slope of slope, a metric reflective of available hard bottom substrate and shelter, becomes the strongest predictor for the presence of characteristic benthic fauna (Pittman et al., 2009). Slope was also indicated to be a strong predictor in the model, although its performance decreased substantially when used by itself. These results indicated that, in the absence of ample sunlight, bottom complexity has significant influence on the presence of deep coral habitat and the species that characterize them. This is consistent with the reported sensitivity of antipatharian (black coral) species to prevailing currents and surrounding seafloor composition as well as depth (Tazioli et al., 2007; Wagner et al., 2012) and previously observed associations between slope of slope, plan curvature, and rugosity on octocoral abundance (Pittman et al., 2009; Sammarco et al., 2016; Woodby et al., 2009; Wedding, Jorgensen, Lepczyk, & Friedlander, 2019) and the relationships predicted in Table 1.

#### 4.1.4 | Soft Bottom

Slope of slope, slope, and depth showed substantial influence on the presence of Soft Bottom habitat. According to the test of permutation importance, model performance decreased by 25.8% (Table 1) when slope of slope was omitted from the model. Furthermore, slope and depth appeared to have substantial predictive influence on the model for Soft Bottom habitat. In the model developed using all environmental predictors, slope of slope had the highest relative influence, although depth was a stronger predictor on its own.

## 5 | CONCLUSIONS

This project utilized the entirety of the ROV-derived dataset from NOAA's 16-year-long endeavour to explore and document seafloor features of the north-western Gulf of Mexico. The results suggest that MaxEnt modelling (as supplemented by MLR to resolve conflicting habitat predictions) is an accurate and useful tool for environmental management bodies interested in preserving the biological integrity of natural marine ecosystems. Specifically, the results of this predictive model show that depth, slope, slope of slope, rugosity, and planform curvature have significant influence on the presence of Coral Reef, Coral Community, Algal Nodule, Algal Reef, Deep Coral, and Soft Bottom habitats described by Schmahl et al. (2008).

By applying this modelling approach and using logistical regression techniques to combine independent models, a series of maps for informing management decisions was created. In the context of this study, these results are particularly relevant to decisions regarding which areas of the north-western Gulf of Mexico should be included in a proposed expansion of the FGBNMS. NOAA researchers have previously confirmed the presence of biologically important habitats and benthic species within the preferred alternative of the FGBNMS boundary expansion proposal (ONMS, 2016); the results of this empirical study suggest that these biologically important habitats are highly likely to be widespread throughout the preferred alternative region (ONMS, 2016). To best inform policy decisions related to FGBNMS boundary expansion, these habitat distribution maps should be subject to future research to refine and validate their depiction of the spatial extent of mesophotic habitats in the northwest Gulf of Mexico. Specifically, to further refine estimates of the extent of biologically important habitats on the reefs and banks in the FGBNMS preferred alternative, the results of this research should be used to target new areas for exploratory work using ROVs, which could be used to ground truth the predicted habitats' extents.

The inclusion of other critical environmental variables and verification of this and forthcoming predictive models will enhance the success of resource management efforts by NOAA and other responsible authorities. It is important to consider that the real distribution of habitats predicted by this model are not explicitly bound by the mathematically derived geographical attributes included in this model. Additionally, the environmental predictors used to develop this model are vulnerable to the inherent error of instruments used to collect data in the marine environment. To address these limitations, future research related to the predictive modelling of these and similar habitats in the north-west Gulf of Mexico should consider incorporating other biological, chemical, and physical properties of the water column that have been empirically shown to influence the growth rate and survival of the benthic species that characterize them. Among these attributes are temperature, salinity, prevalent current direction and speed, nutrients (nitrogen and phosphorous), and turbidity. Built on the observations of unique mesophotic habitats and their associated local geographic characteristics, this model serves as a valid base on which to develop further predictive models with enhanced accuracy by the addition of other contributing variables.

Future studies should also test the methods employed by this research for transferability by applying them to other regions in the Gulf of Mexico and Outer Continental Shelf areas. The results suggest that the methods may be broadly suitable for identifying areas that may contain vital benthic communities that require careful consideration in resource management decisions. The geographic features identified in this study may serve as a useful starting point in developing MaxEnt models for predicting occurrences of benthic habitats across other regions. Similarly, the MLR technique developed here for resolving classification conflicts in 'transitional zones' (areas where multiple habitats are predicted to occur with high probability) may also be transferable to classification conflicts identified in MaxEnt output for other regions.

When management plans for marine protected areas are based on inaccurate or incomplete assessments of benthic habitats, unforeseen environmental consequences may result, potentially contributing to the degradation of habitats and communities beyond recoverable levels. The risk of this occurring can be minimized by incorporating predictive models when developing natural resource policy. MaxEnt models such as that developed here may serve as a cost-effective means of informing management decisions that prioritize the longevity of natural systems. They are a statistically accurate means of finding specific geographic locations where sensitive biological features are likely to occur. Accordingly, these locations and features may be spared from direct and unintended detrimental effects of resource extraction, or other similarly disruptive activities.

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## ORCID

*Travis Keenan Sterne* https://orcid.org/0000-0002-8626-5151

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## APPENDIX A

**TABLE A1** Flower Garden Banks National Marine Sanctuary (FGBNMS) to Coastal and Marine Ecological Classification Standard (CMECS) Habitat Classifications. *Note:* Some components of the CMECS scheme remain consistent throughout all modelled habitats

| | **CMECS Classification** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Geoform** | | **Substrate** | | | **Biotic** | | |
| FGBNMS Classification | **Geoform (Level 2)** | **Geoform Type** | **Substrate Origin** | **Substrate Class** | **Substrate Sub-class** | **Biotic Class** | **Biotic Sub-class** | **Biotic Group** |
| ***Coral Reef*** | Shallow/Mesophotic Coral Reef | Aggregate Coral Reef | Biogenic | Coral | Coral Reef | Reef Biota | Shallow/Mesophotic Coral Reef | Colonized Shallow/Mesophotic Reef |
| ***Coral Community*** | Shallow/Mesophotic Coral Reef | Aggregate Coral Reef | Geologic | Rock | Megaclast | Reef Biota | Shallow/Mesophotic Coral Reef | Colonized Shallow/Mesophotic Reef |
| ***Algal Nodule*** | Shallow/Mesophotic Coral Reef | Aggregate Coral Reef | Biogenic | Algal | Rhodolith | Aquatic Vegetation Bed | Benthic Macroalgae | Crustose Coralline Algae Bed |
| ***Algal (CCA) Reef*** | Shallow/Mesophotic Coral Reef | Aggregate Coral Reef | Geologic | Rock | Megaclast | Reef Biota | Shallow/Mesophotic Coral Reef | Colonized Shallow/Mesophotic Reef |
| ***Deep Reef*** | N/A | Salt Dome | Geologic | Rock | Megaclast | Reef Biota | Shallow/Mesophotic Coral Reef | Colonized Shallow/Mesophotic Reef |
| ***Soft Bottom*** | N/A | Salt Dome | Geologic | Unconsolidated Material | Coarse or Fine | Faunal Bed | Soft Sediment Fauna | N/A |

**TABLE A2** Technical Specifications of remotely operated vehicles used in Data Collection. Details of still camera and navigation equipment onboard the remotely operated vehicles used in data collection by Flower Garden Banks National Marine Sanctuary/ University of North Carolina Wilmington's Undersea Vehicles Program north-western Gulf of Mexico expeditions

| | Super Phantom S2 | MOHAWK |
|---|---|---|
| **Years used/Dives conducted** | 2001–June 2013/339 | October 2013–present/86 |
| **Manufacturer** | Deep Ocean Engineering | Sub-Atlantic-FORUM |
| **Digital still camera** | Nikon Coolpix 995, 3.2mp, 4X zoom, f8, 32 mm lens | Konsberg Maritime OE 14–408, 10mp, 5x zoom, f2.8–4.5, 6.1–30.5-mm lens |
| **Navigation equipment** | ORE Offshore 4410C Trackpoint II Underwater Acoustic Tracking System with an ORE Offshore 4377A transponder with depth telemetry, Northstar 951XD differential GPS, and Azimuth 1000 digital compass. | LinkQuest Tracklink 1500HA, LinkQuest 1505b transponder, Trimble SP461 dual antenna GPS/Heading Receiver. |
| **Location accuracy** | Horizontal Absolute Position Accuracy: ± 0.5% RMS of Slant Range.<br>Slant Range Accuracy: ±1 meter.<br>***Overall horizontal error = 2.70–4.26 m*** | Horizontal Absolute Position Accuracy: ≤0.5% of Slant Range.<br>Slant Range Accuracy:<br>0.2 meter.<br>***Overall horizontal error = 0.25 m + 1 ppm RMS*** |

**TABLE A3** Multinomial logistic regression outcome example

| | | |
|---|---|---|
| (i) | | |
| 1 | AR | -6.2727*** (0.6453) |
| | DC | 0.0262 (0.5396) |
| | _cons | 3.5274*** (0.4034) |
| 2 | AR | Omitted |
| 3 | AR | -10.3518*** (0.6863) |
| | DC | 5.5398*** (0.5989) |
| | _cons | 1.8216*** (0.4637) |
| log likelihood | | -5,742.26 |
| LR chi-square | | 329.23 |
| Pseudo R-square | | 0.03 |
| *N* | | 5,514 |
| (ii) | | |
| 1 | AR | 4.0791*** (0.6898) |
| | DC | -5.9136 (0.6013) |
| | _cons | 1.7059*** (0.4789) |
| 2 | AR | 10.3518*** (0.6863) |
| | DC | -5.9398*** (0.5989) |
| | _cons | -1.8216*** (0.4637) |
| 3 | DC | Omitted |
| log likelihood | | -5,742.26 |
| LR chi-square | | 329.23 |
| Pseudo R-square | | 0.03 |
| *N* | | 5,514 |
| (iii) | | |
| 1 | Other | Omitted |
| 2 | AR | 6.2727*** (0.6453) |
| | DC | -0.0262*** (0.5396) |
| | _cons | -3.5274*** (0.4034) |
| 3 | AR | -4.0791*** (0.6898) |
| | DC | 5.9136*** (0.6013) |
| | _cons | -1.7059*** (0.4789) |
| log likelihood | | -5,742.26 |
| LR chi-square | | 329.23 |
| Pseudo R-square | | 0.03 |
| *N* | | 5,514 |

**p<0.1;* ***p<0.05;* ****p<0.01*

**TABLE A4** Overlapping habitat types, area, and outcome decisions

| Overlapping Distributions | Area (km$^2$) | Outcome |
|---|---|---|
| CC, AN, AR, DC, SB | 0.0016 | DC |
| CR, CC, AN, AR | 0.59 | CR |
| AN, AR, DC, SB | 15.29 | Transitional |
| CR, CC, AN | 0.64 | CR |
| CR, CC, AR | 0.79 | CR |
| CR, AN, AR | 0.92 | CR |
| CC, AN, AR | 0.79 | CC |
| AN, AR, DC | 15.5 | Highest probability |
| AN, AR, SB | 15.36 | Transitional |
| AN, DC, SB | 21.21 | Transitional |
| AR, DC, SB | 35.36 | Transitional |
| CR, CC | 1.57 | Cr |
| CR, AN | 2.66 | Cr |
| CR, AR | 1.14 | Cr |
| CC, AN | 0.85 | Cc |
| CC, AR | 1.01 | Cc |
| CC, DC | 0.002 | Dc |
| CC, SB | 0.002 | Dc |
| AN, AR | 17.58 | Highest probability |
| AN, DC | 21.31 | Highest probability |
| AN, SB | 25.92 | An |
| AR, DC | 35.54 | Highest probability |
| AR, SB | 40.76 | AR |
| DC, SB | 96.37 | DC |

*Note:* Coral Reef (CR), Coral Community (CC), Algal Nodule (AN), Algal Reef (AR), Deep Coral (DC), Soft Bottom (SB). 'Highest Probability' indicates that the habitat in which maximum entropy has predicted the highest probability of occurrence for is assigned to that area/location.